

The University of Chicago

THE MORPHOLOGY
OF SOME AMERICAN SPECIES OF
PSARONIUS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

1937

By
NORMAN JOHN GILLETTE

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE BOTANICAL GAZETTE
Vol. 99, No. 1, September 1937

The University of Chicago

THE MORPHOLOGY
OF SOME AMERICAN SPECIES OF
PSARONIUS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

1937

By
NORMAN JOHN GILLETTE



Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE BOTANICAL GAZETTE
Vol. 99, No. 1, September 1937

MORPHOLOGY OF SOME AMERICAN SPECIES OF PSARONIUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 482

NORMAN J. GILLETTE

(WITH TWENTY FIGURES)

Introduction

Investigations of the genus *Psaronius* Cotta have been numerous, as have been also the investigations of the three form genera *Caulopteris* Lindley and Hutton, *Ptychopteris* Corda, and *Megaphyton* Artis. As early as 1864, STENZEL (25) investigated certain structural aspects of various species of *Psaronius*. ZEILLER (28) studied the fossil flora of the Coal Basin and Permian of Autun and Épinac of France, and described several new species, together with an anatomical description of some. RUDOLPH (23) undertook a comparative investigation of certain species of the genus and some of the living Marattiaceae. In 1906 STENZEL (26) again published a report on the anatomy of certain species, together with a taxonomic review of the more common members of the genus.

Most of the investigations have been made on the European species, and relatively little has been done with the American material. In several instances specimens described as species of *Psaronius* (3, 4, 5, 10, 11, 12) were shown later to be either examples of other genera (8) or the descriptions were altogether inadequate for recognition (17). LESQUEREUX (18) described *Caulopteris giffordi* from Peoria County, Illinois. This specimen was also referred to as *Psaronius giffordi* by POTONIE (22), although no thorough investigation of its structure had been made. FARR (7) described in great detail a fern stem that was collected in Iowa, and appended to his description that of *P. borealis* by MACBRIDE (19) for portions of a stem from the same horizon. Although FARR did not state that his specimen belonged to the same species as MACBRIDE's, the fact that he included in his description that of MACBRIDE indicates that perhaps he considered these two as belonging to the same species.

The roots of *Psaronius* occur commonly in many of the American coal balls (2, 14, 15, 27), but it is only rarely that any stem remains are found in this type of preservation. GRAHAM (9) and NOÉ (20, 21) both mentioned stems of *Psaronius*, but these were not well enough preserved to permit study. Poor preservation is not unusual in coal balls, and the stem size of this tree fern is large. HOSKINS (16), however, described an incomplete specimen of *Psaronius illinoensis* from "a calciferous petrification from the McLeansboro formation of Illinois." This specimen consisted of a narrow zone of roots and a few vascular strands of the stem axis. It was not possible to ascertain the nature of the stem in the living condition, nor could it be associated with any of the larger groups of *Psaronius*.

The several species have been separated into two main groups by HIRMER (13), Distichi and Polystichi, either on the basis of the number of rows of leaves they possessed or on the number of foliar bundles at the periphery of the stem in a given transverse section. A third group, the Incertae, includes those imperfectly known species of which a part or all of the transverse section of the stem is unknown. To the *Psaronii distichi* belongs the genus *Megaphyton*; to the other group *Caulopteris* and *Ptychopteris*. Some species of *Caulopteris* and *Ptychopteris* based on fragmentary specimens would belong to the Incertae if they showed any internal structure.

The *Psaronii polystichi* have been subdivided into the Verticillati and Spirales (13); the species in the former group had their leaves in whorls whereas those in the latter possessed spirally arranged leaves. The main characters used to differentiate the species possessing spirally arranged leaves have been the number of leaf trace bundles appearing at the periphery of any transverse section of the stem, the presence or absence of gum canals in the parenchyma (especially of the woody body), the presence or absence of lacunae in the cortical parenchyma of the roots as well as in the ground parenchyma of the stem axis, and the presence or absence and completeness or incompleteness of the sclerenchymatous sheath tissue in and around the woody cylinder.

The plant material described in this paper represents the silicified remains of Paleozoic tree ferns belonging to *Psaronius*. The specimens were collected about 25 years ago by Mr. VIRGINIUS CHASE of

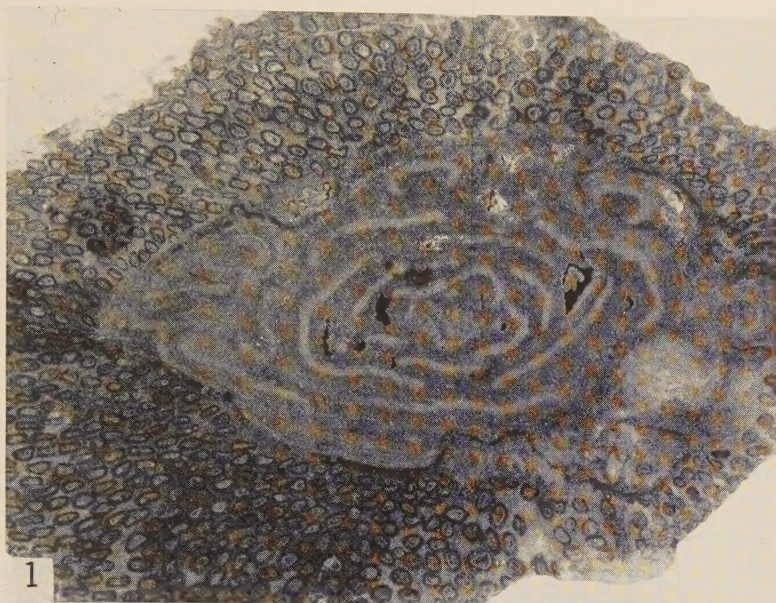
Peoria, Illinois, in a gravel pit in the vicinity of Peoria. This gravel pit has been abandoned long since. Its geological horizon is not known, but it was probably Pleistocene, and thus these fossils were not found in the strata in which they were originally preserved but were carried to that place by a glacier. Inasmuch as most of the European species of *Psaronius* are Permian, it is possible that these were also, although some species have been described from the Carboniferous. One specimen (no. 32) was collected by Mr. CHASE in Stark County, Illinois, and this may represent a Carboniferous species. The material was obtained from Mr. CHASE by Dr. A. C. NOÉ while the writer assisted him in field work for the Illinois State Geological Survey in the summer of 1935. The specimens are in the possession of the Peoria Academy of Science, and the number after each species refers to the accession number in that collection.

Since these stems were silicified and etching with hydrofluoric acid did not prove successful, the "peel method" of examining them was not possible. Thin sections were prepared, and the polished surface of the rocks examined. The model of the vascular skeleton of *P. septangulatus* Gillette (no. 2) was made from the study of a series of ten sections through a given stem, each section being about 1 cm. in thickness. The more detailed observations of the tissues were made on the thin sections.

Psaronius septangulatus sp. nov. (nos. 2, 5) Figs. 1-12

DIAGNOSIS.—In transverse section seven peripheral bundles alternate with seven foliar bundles. Within this zone several (17-20) strands are arranged more or less spirally. Definite sclerenchymatous sheath around woody body, interrupted opposite divergences of the leaf trace bundles. Ground parenchyma of stem axis dense with scattered gum canals. Leaf scars scattered, 2-2.5 cm. wide, 4-5 cm. high, elliptical, open at base and indefinitely closed at top. Vascular bundle scar large (2.5 cm. long, 1 cm. wide), horseshoe-shaped, in upper two-thirds of leaf scar. Leaves spirally arranged. Phyllotaxy 2/7.

Specimen no. 2 is a portion of a stem 27 cm. long, which in the living condition had a diameter of at least 11.5 cm., including the root zone, although in the state of preservation it is crushed so that its present diameters are 13 and 9 cm. The vascular portion of the



FIGS. 1, 2.—Fig. 1, transverse section of *P. septangulatus* (specimen no. 2) showing vascular cylinder surrounded by zone of adventitious roots. Fig. 2, surface view of *P. septangulatus* (no. 5) showing several leaf scars.

stem itself measures 9 by 5 cm. in diameter. There are few external distinguishing characters. The entire stem is covered with adventitious roots; no leaf scars are discernible. The vascular bundle scars of the leaf, as observations of the sectioned material show, are approximately 2.5 cm. long, 1 cm. wide, about 8.5 cm. from center to center on the same vertical row, and the vertical rows 3-3.5 cm. apart. The roots, somewhat intertwined around one another down the stem, give the surface of the stem a fluted appearance. The trees probably reached a height of over 10 meters (13), and the lower portion of the trunk was covered with a dense growth of adventitious roots.

Specimen no. 5 (fig. 2) is a flattened stem about 9 by 5.5 cm. in diameter and 19 cm. long. The petiolar scars, definitely marked on one side of the specimen, are separated from one another by about 2 cm. or less in the same vertical row and by about 2 cm. from side to side. The scar corresponding to the leaf bundle is elliptical, but the upper portion is open and its edges curve inwardly on themselves. The lower portion of the vascular scar is elevated above the surface of the rest of the leaf scar. The surface of the stem contains scattered pits which probably correspond to the divergences of the adventitious roots. These pits are especially prominent on the ridges between the leaf scars. Because of its external nature the specimen is associated with the genus *Caulopteris*.

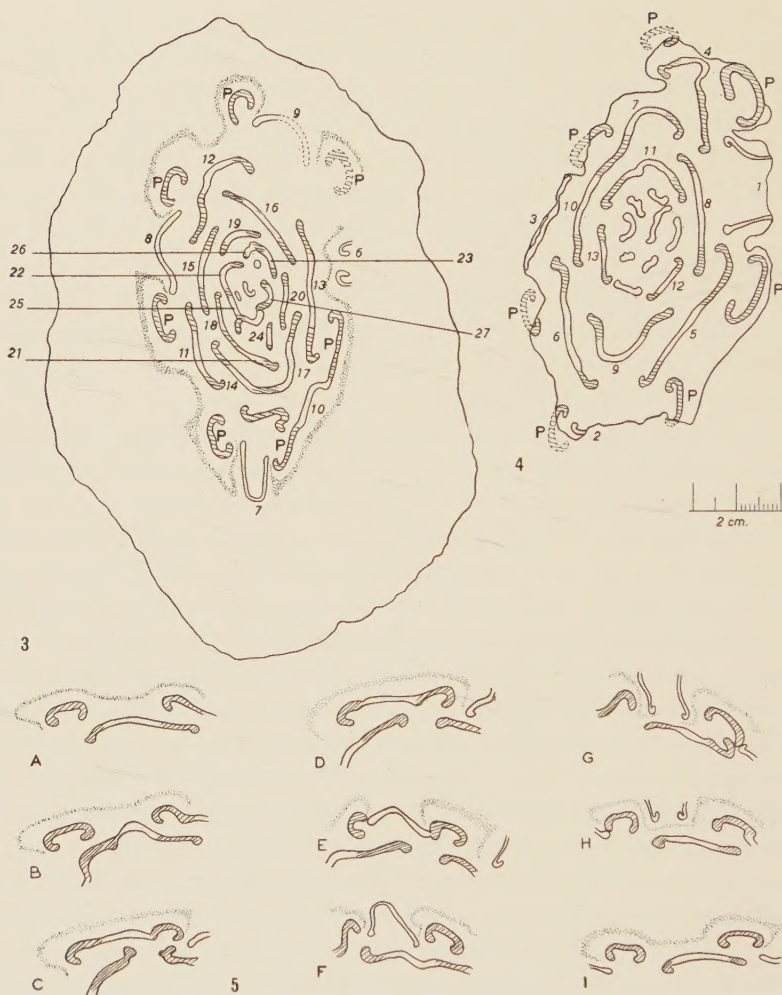
The peripheral bundles are rather strongly arched, with their edges curved inwardly. The tissue surrounding the xylem portion of the vascular strands is differentiated from that of the ground parenchyma. This was probably the phloem, although it is very poorly preserved, and it appears to encircle the xylem. The protoxylem is probably represented by groups of small cells on the inside of the vascular bands (fig. 12). Thus the stem would have been endarch. The parenchyma in which the vascular strands are imbedded is somewhat loosely arranged, although it is rather definitely not lacunar. Occasionally there are small groups of sclerenchymatous tissue near the periphery of the stem. There is no definite sheath, but if there had been one external to the peripheral bundles it probably would have been weathered away. Some of the parenchymatous cells are much larger than others, the larger ones con-

taining some deposited substance. These represent either tannin cells or the so-called gum canals. In general the cellular nature of the vascular tissue is better preserved in this specimen than in no. 2.

This species most closely resembles *P. spissus* Stenzel, but it may be distinguished from it by its greater number of peripheral bundles, five in *P. spissus* and seven in *P. septangulatus*. The woody body of the former species is somewhat smaller in diameter, and the peripheral bundles are separated from the ones on the inside by sclerenchymatous plates. This species differs from *P. demolei* Renault, *P. haidingeri* Stenzel, and *P. espargeollensis* Renault in the non-lacunar nature of the parenchyma as well as in the number of peripheral bundles.

VASCULAR ANATOMY.—(This description is based largely on observations made on specimen no. 2.) In transverse section (figs. 1, 3) the vascular portion of the stem shows a number of conducting strands imbedded in the ground parenchyma of the axis and which seem to be of at least three different types. Around the periphery of the vascular cylinder there are fourteen strands. These are alternately seven peripheral bundles (Randbündel of STENZEL) and seven foliar bundles (Blattbündel). At some levels, however, some of the peripheral bundles and foliar bundles are non-diverged from one another so that there may appear to be fewer than fourteen strands. Within this outer zone of vascular strands there are about sixteen other bundles (the Ersatzbündel and Innere Leitbündel of STENZEL). In transverse section these strands are elongate, platelike, more or less arched toward the center of the stem, and are arranged somewhat spirally in about five coils. Toward the center of the axis they become shorter in their transverse direction, and they are more closely associated. The small strands in the very center seem to have diverged from adjoining strands. In this way it is assumed that new leaf trace bundles may have arisen at the center of the stem. An examination of a series of transverse and longitudinal sections shows that the vascular system is constructed of a network of vascular strands anastomosing and diverging at various places (figs. 6, 7). The significance of these anastomoses and divergences is discussed in detail later.

The peripheral bundles are arched toward the center of the stem,



FIGS. 3-5.—Fig. 3, transverse section of *P. septangulatus* (specimen no. 2) showing vascular cylinder. Leaf trace bundles unlined and numbered 6-27; peripheral bundles (*P*) and other cauline bundles lined. Sclerenchymatous tissue stippled. Root zone outside of sheath. This drawing is from same transverse section as fig. 1 and represents level at top of schematic diagrams of figs. 6 and 7. Fig. 4, transverse section of *P. septangulatus* (no. 5) showing vascular strands. Peripheral bundles (*P*) and other cauline strands lined, foliar strands unlined. Bundles shown by broken lines represent reconstructions. Figs. 3 and 4 both drawn to same scale. Fig. 5, series of diagrams showing divergence of leaf trace from zone of steles just inside peripheral zone to base of petiole. Cauline strands lined, foliar parts unlined, sclerenchyma stippled.

and their lateral edges are strongly incurved. These measure about 8 to 15 mm. along the circumference of the stem. The part these bundles play in the formation of the foliar strands will be considered later.

Alternating with the seven peripheral strands are the foliar bundles. The edges of these latter may still be non-diverged from the

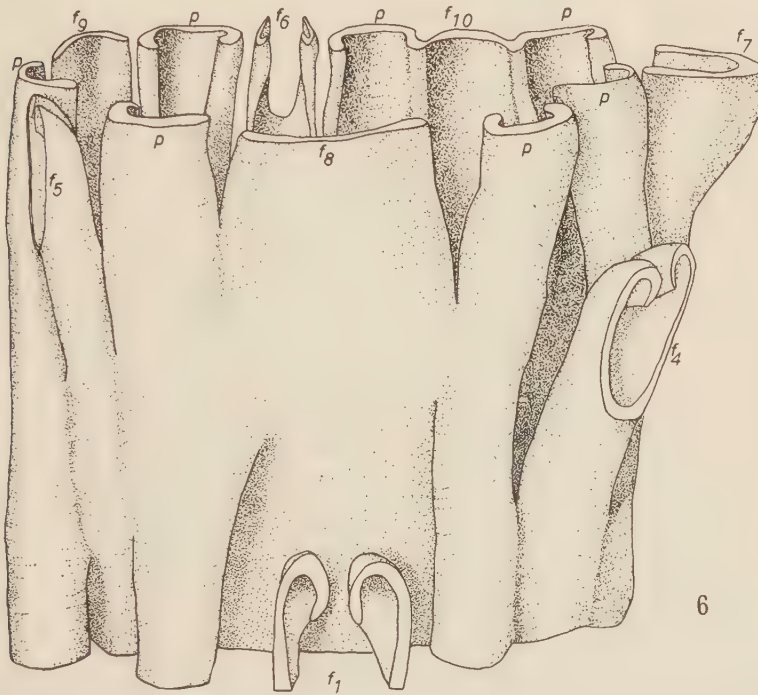


FIG. 6.—Schematic diagram of peripheral portion of vascular skeleton of *P. septangulatus* showing anastomoses of leaf traces with peripheral steles and subsequent divergence into bases of leaves. Peripheral bundles, *P*; foliar strands, *f*₁, *f*₄–*f*₁₀.

peripheral bundles in certain of the transverse sections. In the peripheral region of the woody body any foliar bundle may vary in form, from a plate parallel to the circumference of the stem, to a U-shaped strand with its free ends toward the stem center, to finally two apparently separate strands with the innermost edges curved toward each other, forming J-shaped strands (figs. 1, 3). The appearance of the foliar strands in transverse section depends on their

degree of divergence from the stem axis. The petiole bundle is horseshoe-shaped with its free edges curved inward (*cf. Stipitopteris*). Each foliar bundle forms an arc with a diameter of 8 to 15 mm., so that this measure corresponds to the width of the vascular



FIG. 7.—Same as fig. 6, but seen from inside. Vascular tissue dissected away from half of stem to show anastomoses and divergences of foliar strands with cauline strands as these former follow their course outward and upward. Peripheral bundles, *P*; foliar traces numbered with Arabic numerals.

bundle scar of the leaf scar, were it not obscured by the growth of adventitious roots on the outside of the stem. It is possible in this specimen to trace the foliar strands almost to the center of the stem axis. The final divergence of each strand is from the two adjoining

peripheral bundles, but it is clear that before this trace anastomosed with these peripheral strands it diverged from vascular plates lying adjacent to and inward from the peripheral bundles. In its divergence from the Innere Leitbündel (fig. 5) a gap is produced, so that in a section made at a higher level this strand with its gap has the appearance of two separate strands. The gap formed by this trace is made complete by the anastomosis with the leaf trace of the leaf immediately above this one leaf, as this subsequent leaf trace diverges outward from the next inner conducting strands. This formation of leaf gaps by the divergence of leaf traces from the conducting strands and the subsequent completion of these gaps by the anastomoses of the traces of the next higher leaves and the side flanks of the vascular strands continues as the leaf traces diverge outward and upward from near the center of the stem axis. Since there are about five coils in the spiral formed by the vascular bands of the woody body, there are five of these anastomoses and divergences before any given leaf trace bundle reaches the stem periphery. The side flanks of these Innere Leitbündel that do not diverge outward, together with the Randbündel, form the cauline system which continues up the stem.

In growth and maturation of the plant tissues, and especially of the vascular tissue, it seems probable that the center of the stem axis remained undifferentiated long after the more peripheral parts at that level were mature. Thus the undifferentiated and partially meristematic region of the stem axis was in the form of an inverted cone. In this way it is possible to explain the fact that the leaf bundles can be traced so far down the stem, as one follows them to the center of the woody cylinder. If the situation were as pictured, the new leaf trace bundles would arise probably as branches from the innermost complex of vascular strands (or provascular strands at the time of their origin). The angle which this leaf trace makes with the stem axis as it diverges outward and upward is approximately 7° . This means that the leaf trace originating at the center of the stem at any given level will diverge into the petiole approximately 27 cm. higher up the stem, since the diameter of the woody cylinder may be taken as 7 cm.

The origin of the foliar bundles in this species differs somewhat

from that described by ZEILLER (28) for *Psaronius infarctus* Unger var. *hippocrepicus*. According to him the foliar bands always leave the anastomosis of the vascular bands of the woody body nearest the periphery. This of course is as in the present species, but in the specimen examined by ZEILLER it was impossible for him to trace these strands further toward the center of the stem than just this peripheral region. In this case the leaf trace is described as consisting originally of two distinct halves which have their origins in the anastomoses of the peripheral bands, or a branch from these, with one of the bands at the edge of the central region. These two halves are then united into a single plate, the foliar bundle. STENZEL (26), on the other hand, described another variety of the same species, *P. infarctus* var. *quinquangulus*, in which the leaf trace bundles could be seen as portions of the conducting strands of the region just inside the peripheral circle of bundles; in fact it might be possible to follow a given trace even further toward the stem center. RUDOLPH (23) described a condition that supported STENZEL's conception that the anastomoses appearing between the inner vascular strands probably represented the deeper parts of leaf traces. He described three types of vascular bundles in the stem: the foliar strands, other strands running vertically through the stem (these form a part of the cauline system as defined here), and the so-called peripheral bundles of ZEILLER. RUDOLPH described the course of the leaf trace strands as series of anastomoses and divergences from these cauline strands, in a manner similar to that here described.

HIRMER (13) described three types of leaf trace divergences in the *Psaronii* polystichi which possessed whorled leaves, the *Verticillati*. In the one type, for which he used *P. bibractensis* Renault as the example, the leaf trace is derived from the middle of a bundle plate, the side flanks of which form the peripheral bundles of the woody cylinder at the level of divergence of the leaf trace into the petioles. He described these peripheral bundles as ending blindly and disappearing at the edge of the stem. HIRMER thus pictured the vascular tissue as a series of funnels placed one inside the other, each cycle of leaf traces and their associated cauline bundles representing one funnel. In the second type, that of *P. infarctus* Unger, he found supplementary bundles that had no part in the formation

of the leaf trace. The foliar bundles in this type, however, arose in a manner very similar to that just described for *P. bibractensis*. There are thus alternating "secondary funnels" of vascular tissue which contain no part of the foliar system, but which are closely associated with it, and the "primary funnels" which contain the leaf traces. The third type is exemplified by *P. quadrangulus* Stenzel, and it behaves almost the reverse of *P. bibractensis*. In this case the foliar bundle is formed from the edges of the bundle plates, the central portion of each plate forming the peripheral cauline part of the system. Each leaf trace bundle in this case is therefore composed of two halves derived from as many bundle plates of the stem axis. These two halves unite in pairs at their edges and form together a single horseshoe-shaped leaf trace. In this type, as in the other two just described, the whole vascular system is in the form of funnels placed one inside the other.

FARR (7) described a species of *Psaronius* (*P. borealis* Macbride?) from the Upper Carboniferous of Hardin County, Iowa, which possessed eight longitudinal rows of leaves which he stated appeared to be spirally arranged. It appears from his figures, however, that the leaves were probably arranged on the stem in alternating whorls of four leaves each. The description given by FARR agrees only in the larger details with the specimen here described. He stated that it is apparent "that all leaf traces originate from a central strand and after more or less anastomosis proceed individually to their respective leaf bases. . . . In their course they fuse laterally with the leaf traces of the whorl immediately above and that immediately below. In this way two concentric vascular rings are seen to be formed enveloping the central strand." Although FARR does not indicate that the cauline system played any role in the formation of the leaf trace strands, except perhaps a part of the central strand, he mentions that a "horse-shoe-shaped vascular strand extends from the base to the apex of the stem" between the rows of leaves. No mention is made of any sclerenchymatous sheath around the woody cylinder of the stem, nor is the nature of the ground parenchyma indicated.

All these species, *P. quadrangulus*, *P. infarctus*, *P. borealis*, and *P. bibractensis*, are members of the group of *Psaronii* which pos-

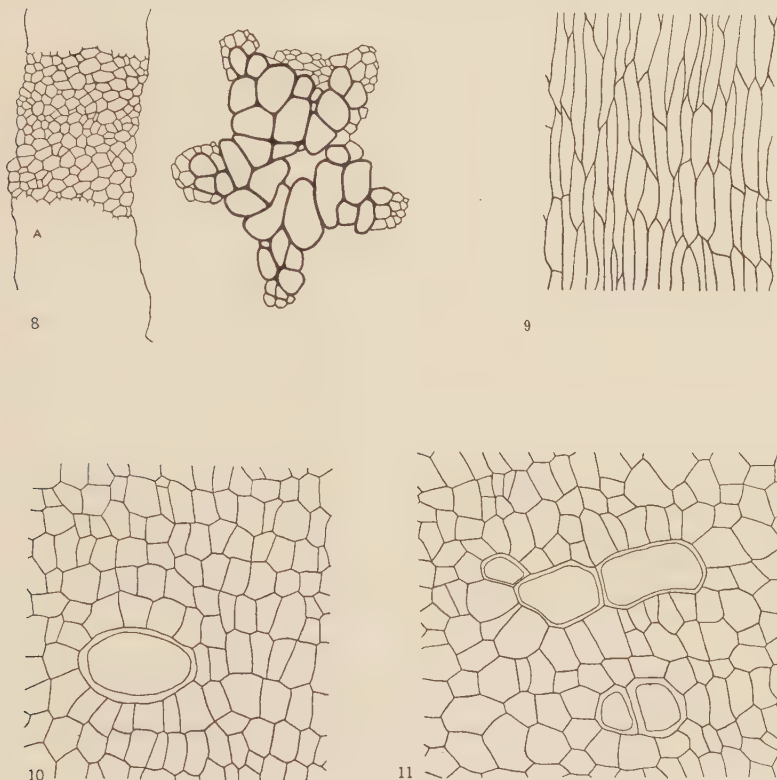
sessed whorled leaves. Little seems to be available concerning the anatomy of those species with spirally arranged leaves. HIRMER is of the opinion that in these species the vascular strands of the woody body are in the form of a "funnel-shaped winding staircase" with the various foliar traces diverging outward as well as upward in the stem. These vascular bands apparently represent the foliar strands as well as the cauline bundles from which these former are derived.

The vascular strands of the stem here described are composed mainly of xylem elements which are rather well preserved in some regions. Where their cellular details are not preserved, they have been infiltrated with a quartz-like material which appears as a contrasting color on the brown ground parenchyma. The xylem is composed of rather large scalariform tracheids which are relatively long with blunt tapering ends. Although no protoxylem has been identified in the longitudinal sections, it is assumed that these stems were either mesarch or endarch, and probably the latter. Around the xylem of the strand there is in some places a tissue that is differentiated from the ground parenchyma. In this region, where any cellular details can be seen they are very small elements with very thin walls. In all probability this represents the phloem region. It is not unusual that this is poorly preserved, because of the nature of the tissue in its living state. In some regions in the stem it is possible to see deposits in the cells of this region, which might represent accumulated food stuffs. This zone of cells seems completely to surround the xylem.

The ground parenchyma of the woody axis is non-lacunar. Its cells are relatively large, thin walled, and isodiametric. Some of the cells contain a deposit of opaque material which may be tannin or some other accumulated plant product. Although there are no lacunae, the cells are not so compact that they form sharp angles in their corners; the reverse is the case, for the cells seem so loosely arranged that each is nearly spherical. These cells vary only slightly in size.

Surrounding the central vascular region is a sheath of sclerenchymatous cells. These are much smaller than either the ground parenchyma of the axis or the xylem tracheids (figs. 8A, 9). Its cells

are compact, somewhat angular, and have thick walls. In longitudinal section they are somewhat elongate and tapering but not nearly so long as are the tracheids. The cells of this sheath are not clearly marked off, either from those within or from those immediately out-



FIGS. 8-11.—Fig. 8, stele of pentarch root of *P. septangulatus* together with some sclerenchymatous tissue of outer cortex of root (A). Fig. 9, longitudinal section of some of cells from sclerenchymatous sheath of *P. septangulatus*. Fig. 10, transverse section of parenchymatous tissue found outside of some of peripheral strands and in leaf scars of *P. septangulatus*. Tissue has appearance of a periderm, and in it are found numerous gum canals. One is shown here. Fig. 11, longitudinal section of same tissue as shown in fig. 8. All figures drawn to same scale.

side it. The sheath is not continuous in the region of the divergences of the leaf trace bundles from the axis.

The roots that surround the woody cylinder are numerous and

pass down the stem in somewhat vertical rows, although there is some intertwining. The steles of these roots are pentarch or hexarch. The xylem in some is rather well preserved, with the large metaxylem in the center and the protoxylem toward the outside (fig. 8). The phloem and the inner cortical parenchyma are not well preserved, but in those regions where some of the inner tissue is preserved it appears to be non-lacunar. The outer region of the root is of thick walled sclerenchymatous cells. These are of the same type as are the cells of the stem sheath; in fact the tissue of the sheath of these roots first appears associated with the steles in the sclerenchymatous sheath of the stem. The vascular elements of the root are derived mainly from the peripheral bundles of the stem, although some may be seen diverging from leaf trace bundles within the peripheral zone. In the root region of some species it is possible to differentiate two separate zones, an inner one in which the roots are imbedded in relatively dense parenchyma, and an outer zone where the roots are more or less free from one another. This specimen shows only one zone of root development.

The parenchyma outside the sclerenchymatous sheath of the roots, in which these are imbedded, consists of somewhat elongate cells in numerous closely intermingled multicellular filaments, having the appearance of a homogeneous tissue; but the filaments seem "combed" in various directions. Concerning the origin of this parenchymatous tissue there have been two main ideas. STENZEL (25, 26) supposed that the inner portion of the zone was a part of the cortex of the stem itself, the roots being intrusive structures. RUDOLPH (23) likewise thought that the regular arrangement of the roots showed that they penetrated a tissue already formed. FARMER and HILL (6) have compared the root zone of the present day Marattiaceae with that of *Psaronius* and found that the root is an intrusive organ in the former, whereas in *Psaronius* the outer cortical region of small-celled sclerenchyma of the root passes almost insensibly into the parenchymatous tissue between them. SOLMS-LAUBACH (24) has shown that the filling-in tissue might have originated from a cellular proliferation at the stem periphery as well as at the root periphery. BERTRAND (1) likewise concluded that this filling-in tissue was "due to a proliferation of a suberose nature, produced at the expense of the superficial tissues."

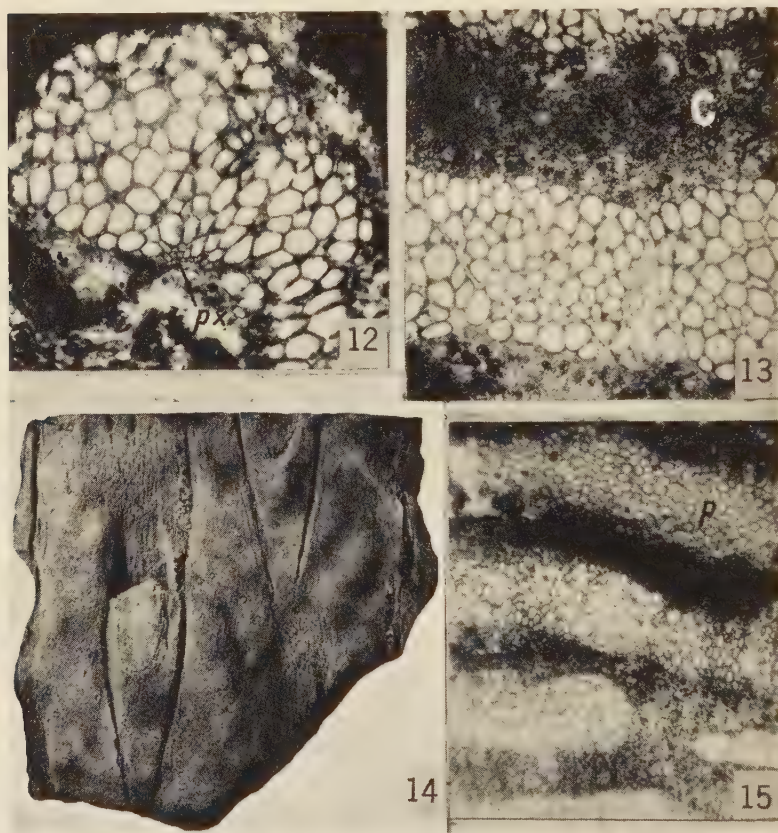
The cells just inside the root zone are differentiated like a periderm (figs. 10, 11). This type of tissue is found especially in the region of a leaf base, but may also be seen outside some of the peripheral bundles. It would appear that in the former case it was formed at the time of leaf fall, or just subsequent to it. It was probably developing at the time the roots were descending on the stem outside it, and by means of this periderm-like growth the irregularities in the stem circumference due to grooves, ribs, etc. were smoothed out by the time the roots were developed at that level. Since the cells in this zone have such a definite orientation, it is possible to detect definite gum canals which could not be identified with certainty in the more loosely arranged ground parenchyma of the woody axis.

Psaronius peoriensis sp. nov. (no. 3) Figs. 14-16

DIAGNOSIS.—In transverse section seven peripheral strands alternate with seven foliar strands; within the peripheral zone about forty vascular strands. No definite sclerenchymatous sheath, but regions of sclerenchymatous tissue associated with the outer vascular strands. Parenchyma of woody body somewhat loose but not lacunar; gum canals scattered and few in number. Leaves rather separated; leaf scars subcontinuous, elongate, tapering at both ends, 10 cm. long, 2 cm. wide. Vascular bundle scar centrally located in leaf scar. Leaves spirally arranged. Phyllotaxy 2/7.

Specimen no. 3 is a flattened stem fragment 8 by 4 cm. in diameter and about 10 cm. long. The scars of the petioles on the external surface are arranged in approximately longitudinal rows. The scars corresponding to the vascular bundles are elliptical, 10-14 mm. wide and approximately 4 cm. long. These are probably open at their upper end with their free ends curved inwardly. The vascular scar is located about in the center of the leaf scar. The scars in the same vertical row are almost joined end to end, the rows themselves being 4 cm. apart from axis to axis. The surface of the stem between the scars is not smooth, but is covered with somewhat elongated but only slightly elevated warts. The verrucose nature can also be seen in some of the petiole regions where the outer portions of the scars have been destroyed. The bases of the adventi-

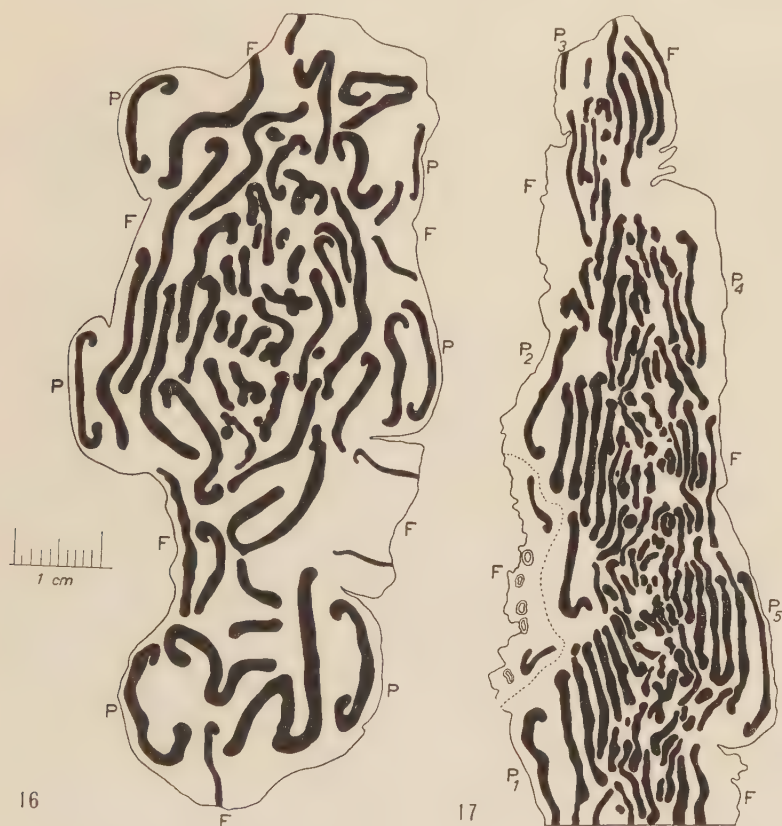
tious roots can be seen in various scattered places, especially in the regions outside the leaf scars.



FIGS. 12-15.—Fig. 12, transverse section of portion of vascular strand of *P. septangulatus* (specimen no. 5) showing protoxylem (*px*); endarch condition. Fig. 13, transverse section of portions of vascular strands of *P. giffordii* showing xylem tracheids. Some tannin cells (?) or gum canals appear as large dark round cells (*C*). Fig. 14, surface view of *P. peoriensis* (specimen no. 3). Fig. 15, transverse section of portion of stem of *P. peoriensis* showing portions of three vascular strands and some of ground parenchyma of axis (*P*).

In transverse section (fig. 16) there are clearly six peripheral bundles, but there were probably seven of these bundles alternating with the seven foliar strands, since the leaves were definitely not

whorled, nor did they have a phyllotaxy of $1/6$. The vascular strands within the peripheral zone vary greatly in their transverse direction from circular strands to long bandlike strands. The foliar bundles do not seem to be very closely associated with the periph-



FIGS. 16, 17.—Fig. 16, transverse section of *P. peoriensis*. Peripheral bundles, *P* leaf traces, *F*. Fig. 17, transverse section of *P. giffordii*. Peripheral bundles, *P*₁–*P*₅. Both figures drawn to same scale.

eral strands in their divergence from the woody body; at least in the one transverse section there was no non-divergence of foliar strands from the peripheral strands as in most of the sections of the other species. The protoxylem of the vascular strands appears to be located on the inside of the curved vascular strands, and

in transverse section appears as groups of small cells. On the outside of these vascular bands in some places cells have been identified as phloem cells. These are not well preserved, however, and they are not present on the outer surface of all the vascular bands, although the tissue in that region has a different appearance from that of the ground parenchyma in those where the phloem is not preserved. This region occupied by the phloem is very narrow in comparison to that occupied by the xylem. The larger cells of this region and some of the cells of the ground parenchyma of the woody body appear to be filled with a dense black substance. This may be tannin or some other substance deposited in these cells.

Psaronius giffordii Potonié (no. 32) Figs. 13, 17-20

DIAGNOSIS.—In transverse section six peripheral bundles alternate with six foliar bundles. Other strands very numerous, approximately 100, arranged more or less in six groups opposite the six peripheral bundles. Parenchyma. . . . Numerous very large cells which may be gum canals. Leaf scars elliptical, open at the top as a horseshoe, 2-2.5 cm. wide, 4 cm. long, subcontinuous in the vertical rows. Vascular bundle scar in upper two-thirds of the leaf scar, horseshoe-shaped. Leaves in alternating whorls of three leaves each.

This specimen is the crushed portion of a stem showing in all nine leaf scars (which are arranged in six vertical rows) the members of alternating rows apparently forming the various whorls of leaves. Each whorl thus contained three members. The rows of leaf scars are about 4.5 cm. apart from center to center. The scars themselves are less than 1 cm. apart in any vertical row. The vascular bundle scars measure 14 mm. in width and 25 mm. in length. The tissue outside the petiolar scars contains sparsely separated pits corresponding to the divergences of the small adventitious roots. In addition to these larger pits the surface of the stem is finely grained. On one side of the specimen the root zone is still partially intact, especially over the rows of leaf scars. In this region it is possible to see the small adventitious roots imbedded in their matrix. These roots do not run parallel down the stem but are intertwined about one another.

In transverse section the numerous vascular strands are so closely

associated that it is difficult to determine anything about the origin of the leaf traces, etc. (fig. 17). The peripheral bundles around the edge of the stem, however, do alternate with the foliar traces as in the other species described. In general there seems to be more regularity of arrangement of the vascular strands opposite the



FIGS. 18-20.—Figs. 18, 19, views of the two surfaces of *P. giffordi* showing leaf scars. In fig. 19 the root mantle covers the leaf scars. Fig 20, longitudinal section of xylem tracheids of *P. giffordi* showing scalariform thickenings on walls.

peripheral bundles than opposite the foliar bundles. There thus appears in the stem in groups radiating from the center toward several of the peripheral bundles at least four definite groups at P_1 , P_2 , P_4 , and P_5 . Because of the crushed nature of the stem this group is not evident opposite P_3 . The portion of the stem including P_6 is not present in this specimen, but it is assumed that there are six peripheral strands because of the apparent location of the center of the stem axis, and because of the whorled arrangement of the leaves.

The general construction of the woody body of this species may

have been similar to that described by HIRMER (13) for *P. infarctus*, in which there were present parallel to the bundle plates giving rise to the leaf traces "secondary bundle funnels" which had nothing to do with the emission of the leaf trace. Because of the nature of the preservation of this specimen it is not possible to determine anything concerning the origin of the leaf traces, as already pointed out. *P. infarctus* was a much larger stem, however, there being five to seven leaves in each whorl, so that there were ten to fourteen peripheral bundles.

The cellular nature of the xylem portion of the vascular strands is especially well preserved (figs. 13, 20). It is composed of relatively large tracheids which have scalariform markings on their longitudinal walls. The woody cylinder was surrounded by a rather indefinite sclerenchymatous sheath, but this had been destroyed in some regions of the stem. In the longitudinal section of the stem cut at right angles to the long diameter of the crushed stem, the vascular strands can be traced the whole length (6 cm.) of the section without anastomosis or branching. The ground parenchyma in which the vascular strands are imbedded is much crushed and poorly preserved, but it appears to have been of a dense nature. In some places, however, there are large spherical cells that seem to contain some sort of deposition substance. These may be what some interpreted as gum canals, or on the other hand they may represent tannin cells.

The external character of this specimen agrees rather closely with that of *Caulopteris giffordi* Lesquereux (18), except for the larger size of the scars of this latter. Inasmuch as no anatomical study has ever been made of *C. giffordi*, the correlation between the internal structures is not possible. POTONIÉ (22) called the internal portion of *C. giffordi* *Psaronius giffordi*. The specimen here described has been compared with the type specimen of LESQUEREUX's species, specimen no. 41006 in the paleobotanical collection in Walker Museum.

Summary

1. A morphological study of four specimens of the Paleozoic tree fern *Psaronius* was made. These specimens were placed in the following three species: *Psaronius septangulatus* Gillette, *P. peoriensis*

Gillette, and *P. giffordi* Potonié. *P. septangulatus* and *P. peoriensis* possessed seven rows of leaves arranged spirally; *P. giffordi* possessed six rows of leaves arranged in two whorls.

2. The vascular anatomy of one of the specimens of *Psaronius septangulatus* was studied in detail from a series of transverse sections of the stem. The leaf traces diverge outward from the center of the stem axis in a manner somewhat similar to that described for *P. infarctus*, which possessed whorled leaves.

3. Thin sections of all three species were examined and described for the different tissue types.

The writer is indebted to Mr. VIRGINIUS CHASE of the Peoria Academy of Science for the material used in this study. Thanks are due also to Dr. A. C. NOÉ for helpful suggestions and criticism during the progress of the work.

DEPARTMENT OF BOTANY
UNIVERSITY OF IDAHO
MOSCOW, IDAHO

LITERATURE CITED

1. BERTRAND, P., L'étude anatomique des fougères anciennes et les problèmes qu'elle soulève. Chap. VII. Problèmes relatifs aux Psaroniées. *Progressus rei Botanicae* 4:281-296. 1913.
2. CROCKER, W. LOUISE, Morphological studies of some Illinois coal ball plants. Unpublished Master's thesis, Department of Botany, Syracuse University. 1933.
3. DAWSON, J. W., On new tree ferns and other fossils from the Devonian. *Quart. Jour. Geol. Soc. London* 27:269-275. 1871.
4. ———, The fossil plants of the Devonian and Upper Silurian formations of Canada. Part I. *Geol. Survey of Canada*. Montreal and London. 1871.
5. ———, Notes on new Erian (Devonian) plants. *Quart. Jour. Geol. Soc. London* 37:299-308. 1881.
6. FARMER, J. B., and HILL, T. G., On the arrangement and structure of the vascular strands in *Angiopteris evecta*, and some other Marattiaceae. *Ann. Bot.* 16:371-402. 1902.
7. FARR, C. H., Notes on a fossil tree-fern of Iowa. *Proc. Iowa Acad. Sci.* 21:59-65. 1914.
8. GOLDRING, WINIFRED, The oldest known petrified forest. *Scientific Monthly* 24:514-529. 1927.
9. GRAHAM, ROY, Pennsylvanian flora of Illinois as revealed in coal balls. II. *BOT. GAZ.* 97:156-168. 1935.

10. HERZER, H., *Psaronius*. 5th Ann. Report, Ohio State Acad. Sci. 1:55-58. 1897.
11. ———, Six new species, including two new genera, of fossil plants. 9th Ann. Report, Ohio State Acad. Sci. 3:22-29. 1900.
12. ———, New fossil plants from the Carboniferous and Devonian. 10th Ann. Report, Ohio State Acad. Sci. 3:40-48. 1901.
13. HIRMER, M., Handbuch der Paläobotanik, I. München and Berlin. 1927.
14. HOSKINS, J. H., Notes on the structure of Pennsylvanian plants from Illinois. II. BOT. GAZ. 85:74-82. 1928.
15. ———, Contributions to the coal measure flora of Illinois. Amer. Mid. Nat. 12:154-163. 1930.
16. ———, *Psaronius illinoensis*. Amer. Mid. Nat. 15:358-362. 1934.
17. KNOWLTON, K. H., Six new species. Science n.s. 16:273-274. 1902.
18. LESQUEREUX, LEO, Description of the coal flora of the Carboniferous formation in Pennsylvania and throughout the United States. Vol. I. 2nd Geol. Survey of Pennsylvania. 336-354. 1880.
19. MACBRIDE, T. H., On certain fossil plant remains in the Iowa herbarium. Proc. Davenport Acad. Sci. 10:153-162. 1904-1906.
20. NOÉ, A. C., Coal ball floras of Illinois. Trans. Illinois State Acad. Sci. 23:429. 1931.
21. ———, Review of American coal ball studies. Trans. Illinois State Acad. Sci. 24:317-320. 1931.
22. POTONIÉ, H., Lehrbuch der Pflanzenpalaeontologie. Berlin. 1899.
23. RUDOLPH, K., Psaronien und Marattiaceen. Vergleichend-anatomische Untersuchung. Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse. Wien 78:165-201. 1906.
24. SOLMS-LAUBACH, H., Der tiefschwarze *Psaronius Haidingeri* von Manebach in Thüringen. Zeitschr. Bot. 3:721-757. 1911.
25. STENZEL, G., in GÖPPERT, H. R., Die fossile Flora der Permischen Formation. Palaeontographica 12:46-82. 1864.
26. ———, Die Psaronien, Beobachtungen und Betrachtungen. Beitr. Paläontologie und Geologie Österreich-Ungarns und des Orients. 19:85-123. 1906.
27. UNDERWOOD, MARY E., Morphology of some Illinois coal ball plants. Unpublished Master's thesis, Department of Botany, Syracuse University. 1934.
28. ZEILLER, R., Bassin houiller et Permien d'Autun et d'Épinac. Flore fossile. Études des gîtes minéraux de la France 2:178-271. 1890.

